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Effects of body temperature on initial bite force in three species of rock- and crevice-dwelling lizards from Mexico

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Abstract

Bite force can be an important aspect of a lizard's organismal performance, and is likely to be subject to influence by ambient conditions including an individual's thermal environment. We examined the effects of body temperature (T_b) on initial bite force of rock- and crevice-dwelling individuals of three species of lizards: *Abronia graminea* (Anguidae), *Barisia imbricata* (Anguidae), and *Xenosaurus fractus* (Xenosauridae) from Mexico. In *B. imbricata* and *X. fractus* from one site (Xochititan, Puebla) initial bite force was greatest at intermediate T_b. In contrast, *X. fractus* from a second site (Tlatlauquitepec, Puebla) showed a weak tendency for initial bite force to increase with T_b. Initial bite force in *A. graminea* was not affected by T_b. Taking our results together, we infer that initial bite force in rock- or crevice-dwelling lizards is often, but not always, related to T_b.

Key Words

Abronia graminea, *Barisia imbricata*, bite force, *Xenosaurus fractus*

Introduction

For lizards, bite force, especially initial bite force, can be an important aspect of organismal performance. For example, bite force can play a role in determining the spectrum of prey an individual can consume (Meyers and Irschick 2015; da Silva et al. 2016; Dollion et al. 2017). In other cases, bite force can be important in determining the outcome of social interactions, whether that is mating/courtship, territoriality, aggressive behavior, or male-male combat (Lappin and Husak 2005; Donihue et al. 2016; Tseng et al. 2019). Thus, understanding what explains variation in bite force within and among species can be important for understanding variation in other aspects of organismal performance.

Body temperature can also potentially affect bite force in lizards. In general, maximal bite forces in ectotherms tend to increase with or peak at an optimal body temperature (Anderson et al. 2008) and thermal acclimation can affect skeletal muscle performance (James 2013). Indeed, body temperature has been shown to affect the performance of jaw muscles in agamid lizards (Herrel et

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al. 1999). However, bite force in some lizards is relatively unaffected by body temperature (Herrel et al. 2007; Cameron et al. 2018; Baxter-Gilbert and Whiting 2019), although there can be a significant drop in performance at the lowest body temperatures (Cameron et al. 2018).

Here, we examined the effects of temperature on initial bite force of rock-dwelling and crevice-dwelling individuals of three species of lizards: Terrestrial Arboreal Alligator Lizard, *Abronia graminea* (Anguidae); Imbricate Alligator Lizard, *Barisia imbricata* (Anguidae), and *Xenosaurus fractus* (Xenosauridae) from Mexico (Figure 1). *Xenosaurus*, especially, are very rarely seen outside their crevices (Lemos-Espinal et al. 2003, 2004; Maciel-Mata et al. 2020). *Abronia graminea* are typically arboreal but some individuals in some populations, including the one studied here, make extensive use of rock-related microhabitats, including crevices (G.A. Woolrich-Piña, unpubl. data). Temperature can influence the anti-predator response of lizards, with cooler lizards tending to adopt a fight response (e.g., biting, threatening) rather than a flight response (Hertz et al. 1982; Crowley and Pietruska 1983; Cury de Barros et al. 2010). Given the limited ability for lizards in crevices to thermoregulate and the relatively cool temperatures prevailing in the crevices used by the species in this study, we predict that the individuals would utilize an aggressive fight response rather than an escape response. The ability to bite may also be important in some of these species during intrasexual aggression (e.g., *Barisia imbricata*, Dashevsky et al. 2013; *Xenosaurus* spp., Ballinger et al. 1995; Smith et al. 1997; Herrel et al. 2001). The crevice or rock dwelling habits of these lizards may also be associated with an opportunistic foraging strategy (e.g.,, Woolrich-Piña et al. 2020), and therefore they may need to be able to capture and consume whatever potential prey they encounter regardless of the temperature. Finally, the microhabitat use of these lizards may limit their ability to thermoregulate or raise their body temperature (Woolrich-Piña et al. 2012, 2020). These observations lead us to predict that initial bite force would not be related to body temperature.

Methods

All lizards were collected from the Sierra Nororiental de Puebla (see Woolrich-Piña et al. 2017 for more details). We collected *A. graminea* (N = 16) from rock-related microhabitats in cloud forest in the vicinity of Zacapoaxtla (19°50’27"N, 97°35’5"W; datum = WGS84), 1920 m elevation, and *B. imbricata* (N = 61) from thorn scrub and grassland transition habitat near the municipalities of Zaragoza and Ocotepec (19°38’48"N, 97°36’22"W; datum = WGS84), elevation 2500 m. We collected *X. fractus* from two populations: 1) a transition from cloud forest to pine-oak forest in the vicinity of Xochititan (N = 19), municipality of Tetela de Ocampo (19°53’15"N, 97°45’54"W; datum = WGS84), 1700 m elevation.; and 2) pine-oak forest in Cerro Cabezón (N = 17), near Tlatlauquitepec (19°51’48"N, 97°30’6"W; datum = WGS84), 1900 m elevation.

We measured snout-vent length (SVL) of each lizard with digital calipers (to nearest 0.01 mm). We performed all experiments within 48 h of collection. We used 1.5 m^3 temperature-controlled cabinets to create four temperature treatments (T_c): 17, 20, 25, and 30 °C. We selected these temperature treatments because body, preferred, and environmental temperatures of these lizards are encompassed in this range of temperatures (*X. fractus*: 9–30 °C, Cardona-Botero et al. 2019; Woolrich-Piña et al. 2020; *B. imbricata*, 9.1–36.6 °C; Fierro-Estrada et al. 2019; no data available for *A. graminea*). Prior to the experiments we confirmed that each cabinet maintained the appropriate temperature over time using a data-logging Fluke 54 IIB digital thermometer (Fluke Corporation, Everett, Washington, USA). We randomly assigned individual lizards to a temperature treatment and placed them in individual plastic containers (30 cm × 15 cm × 15 cm) in the appropriate temperature cabinet for 12 hrs. Given the short period in captivity, we did not feed lizards but we did provide water. For *Barisia imbricata* we exposed 16 lizards to 17 °C and 20 °C; 15 to 25 °C, and 14 to 30 °C. For the *Xenosaurus fractus* from Xochititan, we exposed 5 lizards to 17 °C, 20 °C, and 25 °C; and 4 to 30 °C. For the *X. fractus* from Tlatlauquitepec, we exposed 5 lizards to 17 °C and 4 lizards to 20, 25, and 30 °C. We exposed 4 *Abronia graminea* to each of the test temperatures. Each lizard was subjected to only one temperature treatment.

We constructed a bite force (BF) recording device using an Arduino UNO board (Arduino, Ivrea, Italy) and a high accuracy commercial weight sensor (a 5 kg aluminum alloy IP65 single point load cell; type L6D accuracy class C5 [combined error ≤ ± 0.014%] International Organization of Legal Metrology R60 approval; Zemic Europe B.V., Etten-Laur, The Netherlands). We used a precision 24 bit analog-to-digital converter HX711 made by AVIA Semiconductor (AVIA Semi-conductor (Xiamen) Co., Ltd., Xiamen, China) to amplify the signal of the load cell to be processed in the Arduino board. The load cell was attached to a solid steel base that allowed us to fix the device to a table to avoid vibrations. Bite plates were made of steel and coated with leather and EVA foam to prevent injury and allow lizards to bite with full force. We calibrated the bite force meter using standard laboratory reference weights (OIML class E1; maximum permissible error from nominal value at 1 kg is ± 0.5 mg). We transformed the bite force data output into Newtons.

After 12 h of exposure to the different temperatures, we placed each lizard on a wooden platform at the level of the BF meter to prevent the lizard’s mass from influencing the force exerted by the bite. We stimulated lizards to open their mouths by brushing their snouts with the bite bar perpendicular to the recording device and induced them to bite. The gape angle of all lizards was between 50° and 53° as measured with a transparent pro-

tractor. The entire mouth of each lizard (i.e., from the tip of the snout to the junction of the supra and infralabials) was located within the bite bar, resulting in each bite being completed with the entire mouth. We only recorded BF for the first bite. We conducted all BF measurements inside the temperature-controlled cabinets to minimize changes in temperature, and recorded body temperature (T_b) of each lizard (to nearest 0.1°C using a quick-reading cloacal thermometer; Miller and Weber, Inc., Ridgewood, New York, USA) immediately following the BF measurement to minimize stress on individuals that might influence the BF trials.

We obtained residuals of log-transformed BF by regressing them on log-transformed SVL for each species to examine the effects of temperature on BF independent of absolute body size effects (da Silva et al. 2014). To analyze the effect of body temperature (T_b) on residual BF, we used both a linear regression and a polynomial regression (i.e., including T_b and T_b^2 in the regression) using JMP Pro 15.1 (SAS Institute, Cary, North Carolina, USA). We used measured T_b in our analyses rather than T_c to best reflect lizards' actual temperature during the trial. In preliminary analyses, we found no significant differences in residual BF between males and females in any species, thus we pooled them in our analyses. In addition, preliminary analyses found limited effects of HW and no effects of HL on residual BF, and thus we did not include them in our analyses.

Results

A summary of mean SVL and absolute initial bite force is provided for each species in Table 1.

In *Barisia imbricata*, residual BF was not linearly related to T_b ($N = 61$, $r^2 = 0.012$, $P = 0.40$; however, there was a significant polynomial relationship between residual BF and T_b such that residual BF was higher at intermediate T_b (Fig. 1A; $N = 61$, $r^2 = 0.16$, $P = 0.0052$; residual BF = $-7.14 + 0.73T_b - 0.018T_b^2$). The three remaining studies comprise comparatively little data, but can be used for added perspective. For example, there was an apparent trend, albeit statistically non-significant, for a positive linear relationship between residual BF and T_b in *Xenosaurus fractus* from Tlatlauquitepec (Fig. 1B; $N = 17$, $r^2 = 0.21$, $P = 0.066$; residual BF = $-1.20 + 0.06T_b$), and the polyno-

Table 1. Mean (± S.E.) snout-vent length (SVL) and initial bite force (as absolute bite force and residual bite force) for *Barisia imbricata*, *Xenosaurus fractus* from Tlatlauquitepec, *Xenosaurus fractus* from Xochititan, and *Abronia graminea*. *N* is given in parentheses.

	SVL (mm)	Initial Bite Force (N)
B. imbricata (61)	95.4 ± 1.6	5.6 ± 0.5
X. fractus		
Tlatlauquitepec (17)	103.8 ± 2.6	6.9 ± 0.8
Xochititan (19)	96.6 ± 2.4	8.4 ± 0.6
A. graminea (16)	99.8 ± 2.4	6.7 ± 1.0

Figure 1. Photographs of **A)** *Barisia imbricata*, **B)** *Xenosaurus fractus* from Tlatlauquitepec, **C)** *Xenosaurus fractus* from Xochititan, and **D)** *Abronia graminea*. Photo credits: **A:** Guadalupe Yasmín González-González; **B, C, D:** Gerardo Gasca-Roldán.

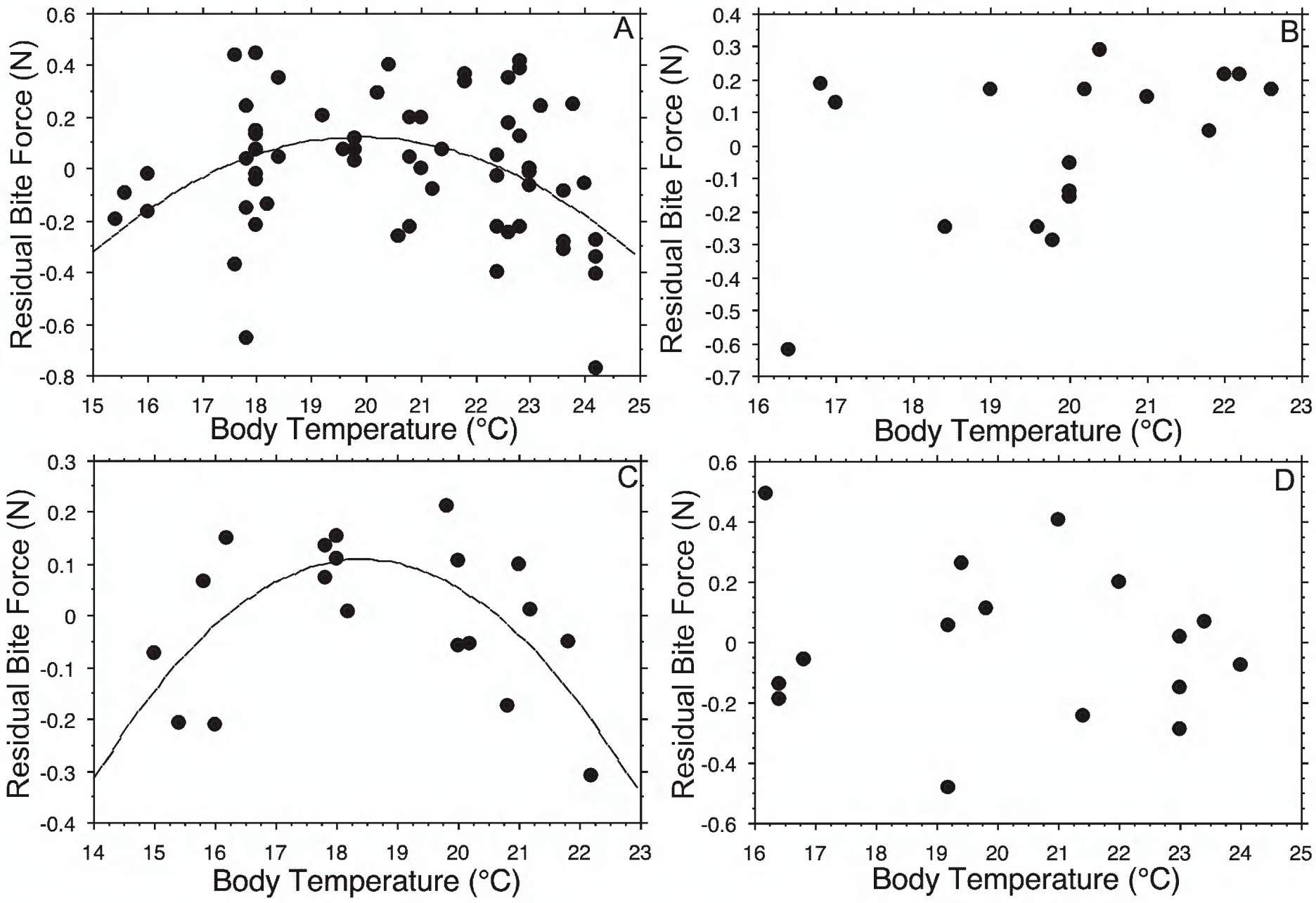

Figure 2. The relationship between residual bite force and body temperature for **A)** *Barisia imbricata*, **B)** *Xenosaurus fractus* from Tlatlauquitepec, **C)** *Xenosaurus fractus* from Xochititan, and **D)** *Abronia graminea*. Lines are provided for significant relationships (A: N = 61, $r^2 = 0.16$, P = 0.0052; residual BF = $-7.14 + 0.73T_b - 0.018T_b^2$; C: N = 19, $r^2 = 0.43$, P = 0.011; residual BF = $-7.28 + 0.80T_b - 0.022T_b^2$).

mial relationship between residual BF and T_b was also not statistically significant (N = 17, $r^2 = 0.22$, P = 0.18). For *X. fractus* from Xochititan, the linear relationship between residual BF and T_b was not significant (N = 19, $r^2 = 0.009$, P = 0.70); however, despite the low sample size, there was a significant polynomial relationship between residual BF and T_b with intermediate T_bs having higher residual BF (Fig. 1C; N = 19, $r^2 = 0.43$, P = 0.011; residual BF = $-7.28 + 0.80T_b - 0.022T_b^2$). Residual BF was not affected by T_b in *Abronia graminea* (Fig. 1D; linear: N = 16, $r^2 = 0.13$, P = 0.67; polynomial: N = 16, $r^2 = 0.018$, P = 0.89), although the sample size was small.

Discussion

The three species of lizards we examined (*A. graminea*, *B. imbricata*, and *X. fractus*) showed different relationships between initial bite force and T_b. There were even differences in this relationship between the two populations of *X. fractus*. Thus, our hypothesis that there would be no relationship between initial bite force and T_b was true for some, but not all, of these species and populations.

In *B. imbricata* initial bite force was highest at intermediate T_b. Mean T_bs of *B. imbricata* from populations in central Mexico range from 17.6 °C to 26.6 °C (Lemos-Espinal et al. 1998; Fierro-Estrada et al. 2019). The preferred body temperatures of *B. imbricata* ranged between 25.0 °C and 31.3 °C (quartile range) (Fierro-Estrada et al. 2019). The range of T_bs where we observed *B. imbricata* to have the greatest initial bite force (17–23 °C) coincides well with the range of observed mean T_bs but is lower than the observed preferred body temperatures, and perhaps initial bite force may be optimized at the T_bs commonly encountered by these lizards.

Initial bite force in *X. fractus* from Xochititan was greatest at intermediate T_b. Mean T_b of *X. fractus* from Xochititan was 19.67 °C (range 10.6–23.8 °C) and preferred body temperature was 21.69 °C (range = 17.7–27.5 °C) (Woolrich-Piña et al. 2020). The peak in initial bite force in *X. fractus* from Xochititan is therefore similar to, but slightly lower than, the mean T_b from previously published field observations, suggesting a match in the initial bite force and T_b experienced in the field. Initial bite force from Tlatlauquitepec showed a weak tendency to increase linearly with body temperature. It thus appears that there might be differences in how initial bite force is affected by T_b in these two populations of *X. fractus*. In addition, absolute BF appears to be greater in *X. fractus* from Xochititan than those from Tlatlauquitepec (see Table 1).

This difference does not appear to be related to SVL since *X. fractus* from Xochititan are smaller than those from Tlatlauquitepec (see Table 1; $F_{1,34} = 4.10$, $P = 0.05$). More study is needed to confirm and explore the explanations for these observed differences.

Initial bite force in *A. graminea* was not affected by T_b. Unfortunately, we are not aware of any field or laboratory studies on T_b in *A. graminea*, or indeed other *Abronia*. We can therefore not relate our results with T_bs of *A. graminea* in nature. However, we infer from the lack of any detectable effect of T_b in our experiment that initial bite force in these lizards is likely to be unaffected by environmental influences on T_b.

In conclusion, based on the one species with robust data, *Barisia imbricata*, initial bite force was greatest in the middle of the range of active body temperatures. A similar pattern was found in *X. fractus* from Xochititan. The other three datasets hint at different relationships between initial bite force and T_b. If the preliminary data on *X. fractus* are supported by larger data sets, then there may be differences in initial bite force, and its relationship with body temperature, between the two populations of *X. fractus*. Overall, our results thus provide mixed support for our hypothesis, and suggest that for at least some of these species, there is a role for temperature in determining initial bite force in these rock- and crevice-dwelling lizards.

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